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SERIE: PLANKTON · BIND III

NR. 3. E. STEEMANN NIELSEN: THE ANNUAL AMOUNT OF ORGANIC MATTER PRODUCED BY THE PHYTOPLANKTON IN THE SOUND OFF HELSINGØR

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I. Introduction.

The production of matter by the phytoplankton, the primary condition of the organic life of the sea, naturally ranges among the principal studying objects of marine biology. The fundamental quantitative phytoplankton investigations in Danish waters were carried out about the beginning of the 20th century by C. G. Joh. Petersen, who collected the material by means of fine-meshed silk nets (C. G. Joh. Petersen, 1898 and 1903).

An investigation on modern principles of the organic matter produced by the phytoplankton of the Danish waters was carried out from October 1932 till October 1933 as continuous investigations off Helsingør in the northern part of the Sound. In the summer of 1931 the introductory methodical investigations had been carried out in the north-western area of the Kattegat at Frederikshavn (Steemann Nielsen, 1932).

Ordinary quantitative determinations of plankton, whether they be carried out as quantitative fishings with net or as determinations after settlement of water samples, only yield information as to the quantity of organisms present. Such investigations do not give any direct measure of the production of matter: the thing measured is the momentary surplus in the metabolism. Actual information on the production of matter is procured through experimental work only. By determination of the oxygen production in bottles containing sea water with the natural contents of organisms it is possible to obtain direct information on the daily production at the different depths of the sea, expressed in mg of organic matter per 1 litre. Gaarder and Gran (1927) were the first to use this method successfully for the determination of the daily production of the phytoplankton. The method has not as yet been extensively used. During the present investigation the method was applied for the first time for the determination of the amount of matter produced annually by the phytoplankton of some area of the sea.

As was expected the northern part of the Sound was not the very best place for an investigation of the present kind on account of the very great changes of hydrographical conditions; nevertheless this locality was chosen owing to the easy communication with the laboratory in Copenhagen. The area off Copenhagen was considered quite unfitted for the purpose because the water of this region generally shows a very high degree of pollution by sewage.

Petersen's investigations (1903) gave reason for the belief that the production of phytoplankton in the Sound was of small extent only: the present investigation proved it to be even smaller than expected, which was of great importance in the experiments that were to constitute the principal basis for the determination of the production of matter. The experiments could not by far be carried out as accurately as is easily done in a more eutrophic water. However, the principal object of interest being naturally the size order of the production of matter, it is a subject of no great importance that the accuracy of the individual experiments is not generally very great.

Figure 1 shows the locality in the Sound at which the investigations were carried out. The depth in this place is 16 m. The water generally shows a pronounced stratification, bottom water and surface water being of quite different origin. As already mentioned, however, the hydrographical conditions are subject to extremely great variations: when the current goes north, the surface water is mostly of Baltic origin; by southerly current it consists of mixed-up water of a much higher salinity.

For the investigation was used a small motor-boat, which was hired from a fisherman at Snekkersten south of Helsingør. Sometimes a rowing boat was used. On the arrival at the place of investigation the anchor was dropped. At first water samples were taken at depths of 0, 5, and 15 m by means of a closing water bottle. The temperature of these depths was measured contemporaneously. A water sample from each depth was preserved with neutral formalin for subsequent counting of the phytoplankton organisms by means of UTERMÖHL's inverted microscope. A water sample of 500 ccm was taken from each depth on the same occasion; these samples were later given over to the Hydrographical Laboratory for determination of Cl, $N\text{-}NO_3$ and P_2O_5. Finally, water samples were treated in the usual way for subsequent determination of oxygen content.

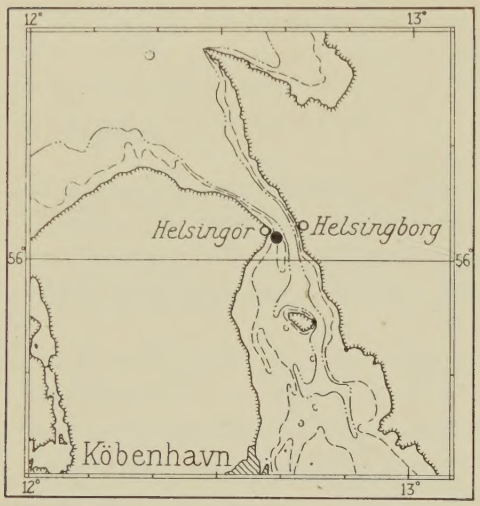

Fig. 1. Chart showing the place in the Sound where the investigations were carried out. The depth curves denotes 10 and 20 m, respectively.

After that a 2 l-glass bottle was filled with surface water; this water was thoroughly stirred and by means of a syphon small 30 ccm bottles with glass stoppers were filled. One bottle was prepared at once for oxygen determination by Winkler's method; the rest of them were lowered to depths of 0.5, 1, 2, 5, 10 and 15 m, 2 bottles at each depth. At various depths were also hung bottles wrapped up in black cloth. The bottles were suspended from a small buoy connected with a larger safely moored buoy. Control experiments were often carried out with water from 5 m depth. This water was taken out by means of a MEYER water bottle.

Furthermore, on the excursions in the autumn of 1932 a thermos bottle holding 1 l was filled with surface water and taken to Copenhagen as quickly as possible where, at the Zoo-physiological Laboratory of the University, assimilation experiments were carried out by artificial light for the purpose of determining the dependence of the CO_2-assimilation on the light.

The bottles that had been suspended from the buoy in the Sound were taken out precisely 24 hours later. To begin with I carried out this work myself; later on the bottles were fetched by the fisherman and sent by train to Copenhagen in a small milk pail, which had been filled with sea water. About two hours after they had been taken out of the sea the bottles arrived at the laboratory, and the reagents could be added to the water.

For the purpose of determining the quantity of zooplankton a haul was made on each excursion from 15 m depth to surface, partly by means of an open conic net of 30 ccm made of gauze no. 9, partly by means of an equally shaped net of gauze no. 25. This zooplankton has not yet been worked.

The investigations were carried out about once a week except in December, January and

February when they were performed every fortnight. The conditions of weather had to be considered, for in the small boat at my disposal it was extremely difficult to work by bad weather. The bottles were lost twice because rough weather came up while they were out. The anchored buoy drifted away when strong current and high sea set in simultaneously. Another time the bottles were lost most probably because a ship had run into the buoy.

During the winter minimum in January and February no metabolism experiments were carried out whereas the rest of the investigations were performed throughout this period. As already mentioned the assimilation experiments in the laboratory were made only in the autumn of 1932.

On account of the very small production of organic matter the determinations of oxygen had to be carried out with the greatest precision, for which provisions were made in several ways. On the whole the oxygen determinations were carried out as by STEEMANN NIELSEN, 1932; special attention is called to the following measures. The 2 l-bottle with the sea water for the experiment was shut with a glass stopper in such a way, that no air-bubbles were found in the bottle, in which some glass balls had been placed before the filling. Now the bottle was shaken for some time, the glass balls causing a thorough stirring of the contents. The small bottles for the experiment were filled as quickly as possible by means of a glass syphon of large diameter. By the adding of NaOH and BaCl it was seen that all bottles were treated in exactly the same way and that exactly the same quantities of substances were added. One hour before the adding of HCl to the oxygen samples the latter were shaken. Each sample was titrated thrice, and readings were made to 0.001 ccm. In taking the mean figure of these three titrations the error of titration is diminished. The 5 ccm used for each titration were measured by means of an adjustable piston pipette of KROGH's invention. In order to get 5ccm it was necessary to take 3 portions with the pipette, the maximum capacity of which was 2 ccm. Towards the end of the investigations it was replaced by a 5ccm automatic KNUDSEN pipette of the same accuracy. It only required a careful cleansing with sulphuric acid before each series of titration.

When the production of matter was very small it was of course impossible to determine with certainty the decrease of the assimilation intensity with the depth. It was only possible to get an approximate value for the production in the surface layers and a rough idea of the depth to which the production could be traced. In this case an ascertainment of the compensation point for the daily production of matter was likewise impossible. The respiration being considerably lower than the assimilation it is even more difficult to obtain the exact values of this process, the measurements of which have therefore generally been totally neglected. A special cause of uncertainty in the determination of the respiration is the fact that we compare two determinations of oxygen, one of which was prepared 24 hours before the other whereas the titrations themselves were carried out at the same time. This circumstance seems to be of some importance when an accuracy like the present is insisted upon.

As a rule two parallel experiments were made with the water from each depth. When the titration of a single bottle fell totally outside the series, either on account of the presence of a larger zooplankton organism or for some other reason, it was rejected. However, the content of zooplankton organisms in the surface water being extremely small the presence of such an organism in the petty quantity of 30 ccm of water is a rare exception, and on the whole this source of error is of inferior importance. Casual errors of titration could be totally eliminated because 3 titrations were carried out with the water of each sample. Some experimental series had to be discarded because accidental outcomes rendered the utilization of the results impossible. Sometimes it was quite impossible to carry out satisfactory titrations, a fact which I

have observed in other marine areas, too. The cause of this phenomenon is unknown to me, but it should be mentioned that it was observed only during the warm season of the year.

It is a great pity that the first attempt at measuring the production of matter by the phytoplankton throughout one year by means of metabolism experiments should have been carried out in a water with so small a production. However, it was possible to measure at any rate the size order of the annual production of matter, and so it must be hoped that this procedure will be applied in other localities, especially in more eutrophic areas where an ascertainment of the size order need not be the only result, but where precise measures of the production of matter at all depths can be obtained. For shorter periods this was carried out i. a. by the author at the Faroes and Iceland and, as already mentioned, in the north-western Kattegat at Frederikshavn in high summer.

The final working of the present material was put off for so long a time principally because the author was of opinion that on the whole the accuracy of the individual metabolism experiments was too small. In a previous publication (Steemann Nielsen, 1935, b) it was even hinted that in a water like the present the method could be safely used only during a phytoplankton maximum.

However, a thorough examination of the whole material of investigation showed that this judgment was much too critical and in fact quite erroneous. It is true that the value of the individual experiments is often of less importance; but if all experiments are taken as a whole for the sole purpose of establishing the size order of the production of matter throughout the year, the thing is quite different. It should be remembered that quite a succession of experimental series were carried out, about 4 every month. For the judgment of the production in its broad features it is therefore of less importance that some of the experimental series had to be rejected on account of failing accuracy. Likewise, it is of no great importance that some other experimental series do not show the production of the individual depths but only the average of the surface layers. Finally: although an error of up to 50 % must be considered possible in some of the experimental series, this is of quite inferior importance for the actual aim of these investigations: the determination of the size order of the annual production of organic matter. In a later section of this treatise (p. 31) it will be shown that the annual production in a more eutrophic area as e.g. the north-western part of the Kattegat is of such an extent, that even a rather large error in the determination of the production in the Sound may be ignored completely in a comparison between the productions of these two waters.

Only an experimental measuring of the production of matter enables us to compare the various marine areas with a view to their production. It is emphasized once more that the ordinary quantitative plankton investigations only give a measure of the momentary surplus, not of the production itself; but it is necessary to know the latter if you want to compare the various marine areas with each other.

Another circumstance is of importance in this connexion. A comparison of two plankton populations on the basis of countings is extremely difficult, more particularly because every population generally consists of a long series of organisms of greatly varying size. It is especially difficult to compare an oceanic plankton, principally consisting of small coccolithophorids and other small species, with a neritic plankton, the bulk of which is often made up of comparatively large diatoms.

If the collectings are carried out with nets made of the finest silk, it is possible to determine volume, content of organic matter or chlorophyll; but a measuring of the phytoplankton by means of net samples should be avoided because only a fractional part of the phytoplankton

is retained by the net; furthermore, the size of this fraction is subject to very great variations (cp. Steemann Nielsen, 1935 b). A determination of the organic matter after settlement of small quantities of water is possible but difficult (v. Brand, 1935).

II. The plankton production in the autumn of 1932 (from October till the end of December.

Throughout this period a measurable production of plankton took place. The nutritive salts, rather considerable quantities of which were now present in the bottom water, could also generally be established at the surface (see Fig. 2). Throughout the autumn amounts of nutritive salts are carried to the surface water, and in most cases the production of phytoplankton is not great enough to cause an immediate exhaustion of the supply of nitrate and phosphate. We saw above that a quantitative plankton sample does not give any proper measure of the plankton production but shows only the momentary surplus; in the same way the quantities of nitrate and phosphate constitute no real standard of the supply and regeneration of these salts. A traceable quantity of nutritive salts only shows that the consumption of these salts during the propagation of the plankton algae cannot keep pace with the supply and regeneration of the salts.

The production of phytoplankton during this period must be characterized as not quite insignificant. However it cannot by far be ranked

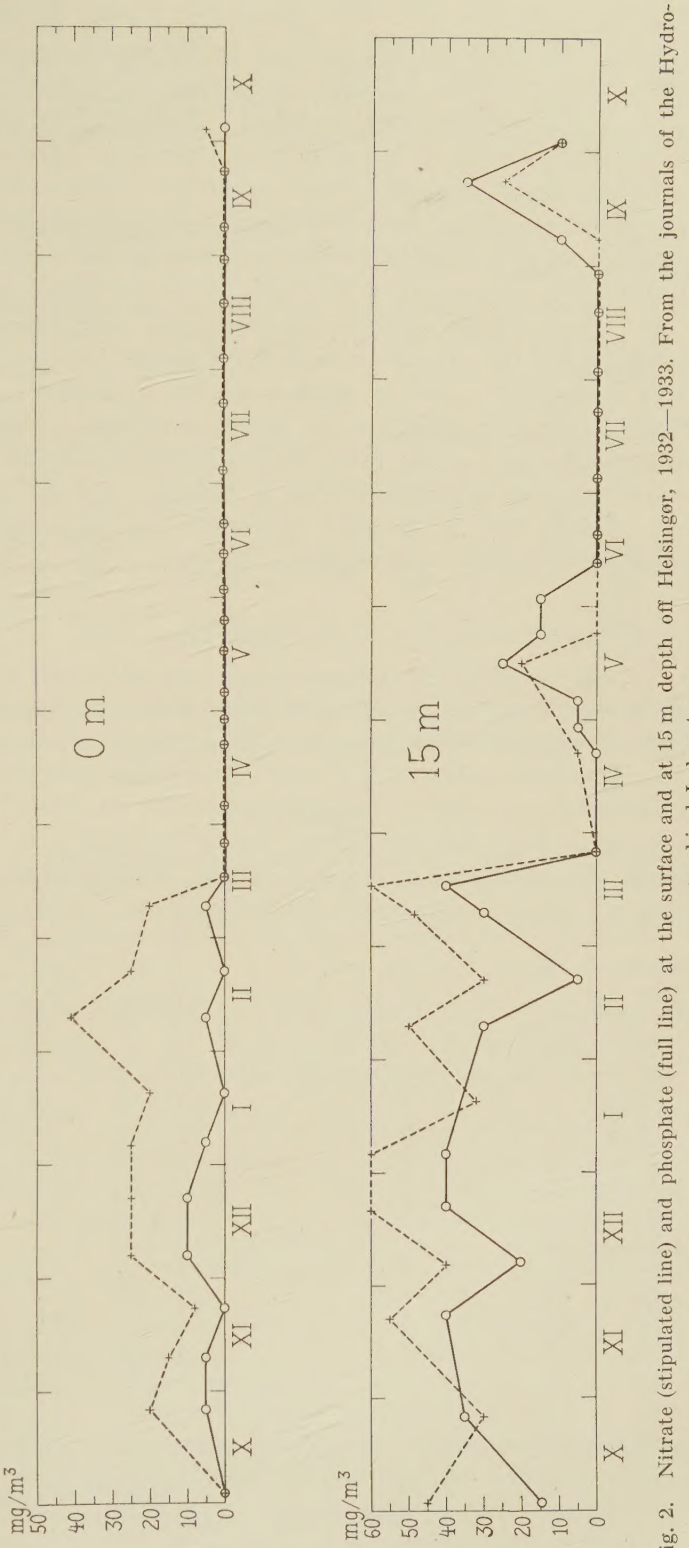

Fig. 2. Nitrate (stipulated line) and phosphate (full line) at the surface and at 15 m depth off Helsingor, 1932—1933. From the journals of the Hydrographical Laboratory.

with the production of a eutrophic area; during the maximum of early summer at the south coast of Iceland or in high summer in the north-western Kattegat off Frederikshavn (Steemann Nielsen 1932) the daily production is about 10 times as large.

It has already been mentioned that the hydrographical conditions are very different according as northerly or southerly currents have prevailed for some time previous. Roughly speaking only the hydrographical conditions of the surface current are of interest for examinations of the amount of matter produced by the phytoplankton in this water because the compensation point for the CO_2-assimilation and respiration is here situated at a very small depth: in most cases it was found at depths of 5—8 m at the highest.

The composition of the plankton was quite different according as Baltic water or water showing a greater admixture from the Kattegat, i.e. more salinous water, was found at surface. Baltic water was found at surface on the excursions of Oct. 11th (9.40 ‰ S.) and Nov. 9th (10.68 ‰ S.). The plankton consisted principally of flagellates (incl. unicellular green algae) and cyanophyceae. The amount of diatoms was quite inferior. The rest of the excursions in autumn showed a predominance of diatoms, and the salinity was always above 14 ‰. It was most obvious that the greatest production of matter occurred when the salter Kattegat water prevailed at surface (see Figure 3, p. 31).

Excursion I, October 3rd (Table 1).

The composition of the plankton was fairly uniform from bottom to surface. The diatoms predominated in the comparatively salt water. In a quantitative respect the rather large-sized species *Leptocylindrus danicus* was of principal importance; further *Sceletonoma costatum* and

Table 1 a.

Content of phytoplankton per 100 ccm on Excursion I, 3. X. 1932.

Depth in m	0	5	15
Temperature, ° C.	12.7	12.9	13.3
Salinity, ‰	15.12	16.28	23.34
P_2O_5, mg/m³	0	0	25
N — NO_3, mg/m³	0	0	45
Peridinians	190	..	60
Diatoms	6,420	..	5,620
Sceletonema costatum	770	..	670
Leptocylindrus danicus	2,840	..	2,240
Rhizosolenia fragilissima	1,020	..	240
Chaetoceros species	650	..	770
Cyanophycé-colonies	80	..	100
Flagellates	4,200	..	r
Distephanus speculum	640	..	50
Infusorians	1,800	..	20

Table 1 b.

Experiments on production of matter in surface water from Excursion I. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.24
1.5	0.20
2.5	0.20
5.5	0.15
10.5	0.00
15.5	0.00

Rhizosolenia fragilissima should be mentioned. Flagellates and cyanophyceae occurred in smaller quantities. The metabolism experiments showed a production per 24 hours in the surface layers of about 0:21 mg glucose per l. The compensation point was found at a depth of 8 m. It was bright sunlight during the experiment.

Excursion II, October 11th (Table 2).

Baltic water was now found in the surface layers and the character of the plankton was quite different. Diatoms were present in extremely small quantities — the brackish water species *Chaetocerus danicus* and a minute Thalassiosira species —. The larger organisms of the October samples were counted in the autumn of the same year whereas the counting of the small flagellates was postponed on account of shortness of settlement glasses with a sufficiently thin bottom. It was impossible to use strong objectives for the settlement glasses originally procured for UTERMÖHL's microscope (see STEEMANN NIELSEN, 1933). When the tiny organisms of the samples were to be counted later on it turned out that a precipitation of some matter had taken place in all three samples from Excursion II, so that a counting was rendered utterly impossible. No doubt a bad formalin must have been used for the preservation of these samples. However, the metabolism experiments showed that autotrophic flagellates must have been present in no small quantities. The production of matter in the upper water layers was about 0.10 mg glucose per l.

Table 2 a.

Content of phytoplankton per 100 ccm on Excursion II, 11. X. 1932.

Depth in m	0	5	12
Temperature, ° C.	11.9	11.9	11.4
Salinity, ‰	..	..	..
P_2O_5, mg m^3	..	..	..
N — NO_3, mg m^3	..	..	..
Peridinians	..	..	20
Diatoms	340	..	900
Thalassiosira sp.	240	..	..
Cyanophycé-colonies	480	..	..
Flagellates	?	..	?
Infusorians	880	..	20

Table 2 b.

Experiments on production of matter in surface water from Excursion II. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.12
2	0.07
5	0.02
10	0.00

At a depth of 15 m were found various diatoms, which had been carried in from the Kattegat by the bottom current. The salinity was here 27.26 ‰.

Excursion III, October 18th (Table 3).

A typical Kattegat plankton was found at all depths. Besides a great many diatoms the peridinians *Ceratium furca*, *C. lineatum*, *C. fusus* and *C. tripos* occurred in comparatively large quantities. As regards production the most important species is no doubt the large diatom *Cerataulina bergonii*.

The metabolism experiments in the

Table 3.

Content of phytoplankton per 100 ccm on Excursion III, 18. X. 1932.

Depth in m	0	5	15
Temperature, ° C.	10.9	11.1	11.4
Salinity, ‰	16.87	17.66	31.23
P_2O_5, mg/m^3	—	0	0
N — NO_3, mg/m^3	—	0	0
Peridinians	720	310	20
Ceratium lineatum	240	180	10
Diatoms	5,880	4,470	6,840
Rhizosolenia alata	250	410	210
Chaetoceros laciniosus	370	600	420
— radians	1,380	110	1,960
Cerataulina bergonii	1,100	1,190	1,720
Flagellates	r	r	r
Distephanus speculum	100	40	50
Infusorians	540	30	30

Sound were spoiled by a sudden storm during which the buoy with the bottles disappeared. However, on the basis of experiments carried out in the laboratory with the surface water (see Figure 6, p. 33) we are able to calculate that the production of the surface layers, assuming that normal conditions of light obtained, must have been about 0.20 mg glucose per l.

Excursion IV, October 25th.

The hydrographical conditions were quite the same as the week before, and both in quantity and composition the plankton corresponded exactly to that found on October 18th.

Table 4 a.

Content of phytoplankton per 100 ccm on Excursion IV, 25. X. 1932.

Depth in m	0	5	15
Temperature, ° C.	10.1	10.3	10.9
Salinity, ‰	20.83	21.62	27.79
P_2O_5, mg m^3	5	5	35
N NO_3, mg m^3	20	25	30
Peridinians	460	180	140
Ceratium lineatum	200	80	30
Diatoms	9,200	6,970	5,440
Sceletonema costatum	1,780	1,560	970
Rhizosolenia alata	500	490	330
Chaetoceros laciniosus	80	560	320
— curvisetus	580	150	580
— radians	600	820	480
Eucampia zoodiacus	620	500	10
Cerataulina bergonii	800	1,070	260
Asterionella japonica	720	20	120
Nitzschia delicatissima	1,300	550	660
Flagellates	r	r	r
Infusorians	220	60	..

Table 4 b.

Experiments on production of matter in surface water from Excursion IV. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.22
1	0.20
2	0.14
5	0.07
10	0.00
15	0.00

The production of matter in the surface layers was about 0.19 mg glucose per l. During the first half of the experiment it was bright sunlight, during the second half a light rain was falling. The compensation point for the daily production of matter was presumably found at a depth of about 6 m.

Excursion V, November 9th (Table 5).

A strong northerly current had been running for some time, and the salinity at surface was only 10.68 ‰. Consequently, the plankton had a Baltic character. A great variety of flagellates with chromatophores (including unicellular green algae) occurred rather abundantly. Of course most of them could not be determined in a preserved state by means of the inverted microscope: this could be done only with forms like a *Carteria* species and *Eutreptia lanowii*. Cyanophyceae played no part whatever.

The weather was rather rough, and as only a rowing boat was available the examinations were on this occasion carried out closer to the shore at the outer poles of the pound nets where

Table 5 a.

Content of phytoplankton per 100 ccm. on Excursion V, 9. XI. 1932.

Depth in m	0	7.5
Temperature, ° C.	7.8	7.6
Salinity, ‰	10.68	10.82
P_2O_5, mg/m³	5	5
$N - NO_3$, mg/m³	15	15
Peridinians	..	10
Diatoms	260	230
Flagellates	10,600	7,200
Eutreptia lanowii	600	400
Infusorians	2,200	20

Table 5 b.

Experiments on production of matter in surface water from Excursion V. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.08
1	0.08
2	0.09
5	0.05
7	0.01

the depth was only 7.5 m. The production of matter in the surface layers was about 0.08 mg glucose per l in 24 hours. The compensation point was presumably found at about 6 m depth.

Excursion VI, November 22nd (Table 6).

On this date the surface salinity was 13.84 ‰. The plankton at surface and 5 m depth was very rich, more than 100,000 diatoms occurring per 100 ccm. The predominant form was *Sceletonoma costatum*; besides *Nitzschia delicatissima* abounded. The nutritive salts of the surface layers were practically exhausted (Figure 2), a result of the intense production.

At the very surface the production of matter was 0.32 mg glucose per l. This is no great production in view of the rich plankton; but it should be remembered that we are dealing with

Table 6 a.

Content of phytoplankton per 100 ccm on Excursion VI, 22. XI. 1932.

Depth in m	0	5	12
Temperature, ° C.	6.5	6.8	11.5
Salinity, ‰	13.84	15.04	32.38
P_2O_5, mg m³	0	5	40
$N - NO_3$, mg m³	8	8	55
Peridinians	900	1,560	..
Diatoms	106,280	110,600	4,890
Sceletonema costatum	88,000	90,000	2,450
Chaetoceros curvisetus	1,880	700	1,870
Nitzschia delicatissima	12,600	14,000	40
Flagellates	4,800	4,000	800
Infusorians	120	..	..

Table 6 b.

Experiments on production of matter in surface water from Excursion VI. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.34
1	—
2	0.17
5	0.04
10	0.00

quite small species and that it is rather late in the year. The weather was bright during the whole experiment. Already at a depth of 1 m the production of matter was now smaller than at the very surface. The compensation point for the daily production is now situated quite close to the surface, at about 5 m depth.

Excursion VII, December 6th (Table 7).

The amount of plankton at surface is now rather small. At depths of 5 and 15 m, however, we find a rich plankton of the same kind as that occurring during the previous excursion.

Table 7 a.

Content of phytoplankton per 100 ccm on Excursion VII, 6. XII. 1932.

Depth in m	0	5	15
Temperature, ° C.	5.6	6.0	7.7
Salinity, ‰	17.59	20.39	25.04
P_2O_5, mg/m³	10	10	20
$N — NO_3$, mg/m³	25	25	40
Peridinians	50	270	30
Diatoms	1,780	24,500	29,900
Sceletonema costatum	260	10,500	14,500
Chaetoceros curvisetus	200	1,440	2,360
Thalassiothrix nitzschioides	360	700	1,840
Nitzschia delicatissima	570	7,700	8,000
Flagellates	2,400	800	400
Infusorians	390	..	10

Table 7 b.

Experiments on production of matter in surface water from Excursion VII. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.05
1	0.03
2	0.00
5	0.00
10	0.00

The plankton production is now about to stop on account of the lateness in the season. The metabolism experiments, which were carried out with surface water, only yielded quite small outcomes. The weather was very dark during the experiment, neither had it been bright during the previous days.

Excursion VIII, December 22nd (Table 8).

The plankton production had not stopped completely in December, for as late as now some plankton is found; as was the case during the last excursion it occurs principally in the deeper water layers. Once more the diatom *Sceletonema costatum* predominated, but at surface and at 5 m depth also some autotrophic flagellates were found.

Table 8.

Content of phytoplankton per 100 ccm on Excursion VIII, 22. XII. 1932.

Depth in m	0	5	15
Temperature, ° C.	4.4	4.4	9.2
Salinity, ‰	15.25	16.00	31.90
P_2O_5, mg/m³	10	10	40
$N — NO_3$, mg/m³	25	25	60
Peridinians	20	40	..
Diatoms	2,180	3,160	21,630
Sceletonema costatum	1,200	2,030	20,000
Nitzschia delicatissima	760	610	680
Flagellates	8,800	7,200	800
Infusorians	90	20	..

The metabolism experiments showed a production too small to be measured. The conditions of light during the experiment were very bad, the weather being cloudy all the time. No doubt it is only by good conditions of light that a real production takes place so late in the year, but in 1932 they cannot have been so very bad during the last months of the year. In 1935, for instance, the phytoplankton of the Sound had disappeared already in the end of November.

This excursion was the last in the winter of 1932—33 in which proper quantities of phytoplankton were found in the Sound.

III. The winter minimum from January to the middle of March.

During this period the phytoplankton was nearly totally absent in all water layers: only quite inconsiderable amounts of flagellates and now and then some few cyanophyceae and diatoms were found. The countings were rendered difficult by the extremely great quantities of detritus suspended in the water during the whole of this period. The few organisms quite disappeared in the masses of detritus. Therefore the results of counting are not stated individually. The size order of the number of plankton algae per 100 ccm was 200 at the highest.

The following excursions were made during this period: Excursion IX, January 5th, Excursion X, January 19th, Excursion XI, February 9th, Excursion XII, February 21st and Excursion XIII, March 9th. In a quantitative respect the conditions of plankton were quite the same, both when Baltic water and Kattegat water prevailed. The amount of nutritive salts was not very great, at surface 10 mg P_2O_5 and 45 mg N_{NO_2} at most; when the Baltic water prevailed, the values were still lower (see Figure 2).

The light in connexion with the poor transparency of the sea water due to the great quantities of detritus mentioned above must be supposed to have been the limiting factor of the production of phytoplankton during this period (see further p. 24).

During the winter minimum no metabolism experiments were carried out until on Excursion XIII on March 9th. Of course this experiment showed no measurable production of matter.

IV. The spring maximum in March.

Excursion XIV, March 16th (Table 9).

On Excursion XIII, March 9th, the phytoplankton was extremely poor; on Excursion XIV, March 16th, a very rich plankton suddenly occurred, showing at surface more than 60,000

Table 9 a.

Content of phytoplankton per 100 ccm on Excursion XIV, 16. III. 1933.

Depth in m	0	5	15
Temperature, ° C.	2.0	2.0	5.5
Salinity, ‰	17.03	17.37	33.18
P_2O_5, mg m³	0	0	40
$N - NO_3$, mg/m³	0	0	60
Peridinians	500	6,500	..
Diatoms	60,050	74,000	350
Sceletonema costatum	9,500	13,500	..
Thalassiosira nordenskjöldii	1,400	4,400	250
Chaetoceros debilis	40,750	46,500	..
Cyanophycé-colonies	1,600	400	..
Flagellates	14,800	5,600	1,600
Infusorians	300	..	..

Table 9 b.

Experiments on production of matter in surface water from Excursion XIV. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.40
1	0.42
2	0.28
5	0.00
10	0.00
15	0.00

diatoms, among them about 40,000 *Chaetoceros debilis*. Further some flagellates, cyanophyceae and peridinians were observed. The plankton at 5 m depth was the same as that found at surface;

at 15 m depth, however, only very few organisms appeared. Nitrate and phosphate could no more be established in the surface layers.

In the course of one week the plankton quantity has increased from a small winter minimum to a strongly marked spring maximum. No doubt the occurrence of a period of sunny days is a contributary cause of the fact that the conditions of the production suddenly rise from a minimum to the present height (cp. p. 24). The difference of the surface salinities on the 9th and the 16th of March shows that the surface water on the two dates is of partially different origin: on the former excursion Baltic water was found at surface; on the latter the typical salter water from the Kattegat prevailed. As will be demonstrated later this fact must be supposed to be the principal cause of the rich development of the phytoplankton established on Excursion XIV.

The metabolism experiments with surface water from this excursion show a production of matter at the very surface of about 41 mg glucose per 24 hours. In view of the comparatively rich plankton this is not very much. However, the conditions of light during the experiment were bad because it was raining almost continually. The poor conditions of light also appear from the fact that the production at 2 m depth is considerably smaller than at the very surface and that the compensation point for the daily production of matter was found at a depth of 4 m at most.

Excursion XV, March 24th (Table 10).

The salinity at surface is considerable lower than on the previous excursion. The composition of the plankton is the same as the week before, but the amount has fallen to about $^1/_5$ of the quantity found on this occasion, the number being about 10,000 diatoms at surface. At 15 m depth, however, where practically no phytoplankton was found on March, 16th, we now find an exceedingly rich plankton with more than 100,000 diatoms per 100 ccm. The principal species is *Chaetoceros debilis* (68,000 ind. per 100 ccm), part of which had formed resting spores. The plankton is about to sink and disappear. The large amount of phytoplankton at a depth of 15 m originates from the surface; at 15 m depth no production of phytoplankton takes place in the Sound. The problems caused by different origin of the water masses are discussed in chapt. VI, p. 24.

Table 10 a.

Content of phytoplankton per 100 ccm on Excursion XV, 24. III. 1933.

Depth in m	0	5	15
Temperature, ° C	3.4	3.5	3.5
Salinity, ‰	11.87	14.79	22.41
P_2O_5, mg/m³	0	0	0
$N — NO_3$, mg/m³	0	10	0
Peridinians	160	360	..
Diatoms	10,120	11,260	107,700
Sceletonema costatum	5,500	3,400	26,000
Chaetoceros debilis	3,100	3,900	68,000
Cyanophycé-colonies	60	40	..
Flagellates	r	r	6,400
Infusorians	40	40	..

Table 10 b.

Experiments on production of matter in surface water from Excursion XV. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.13
2	0.14
5	0.09
10	—
15	0.00

The actual spring maximum is already over. During the previous excursion we found that all nutritive salts had been consumed in the course of one week. From now on throughout the summer the nutritive salts are the limiting factor of the production of phytoplankton. Nutritive salts cannot again be established in the surface layers until October.

The metabolism experiments with surface water also showed a very small production: about 0.12 mg glucose per l in 24 hours. It was bright sunlight during the whole experiment.

Excursion XVI, April 4th (Table 11).

The surface salinity is now about 18.38 ‰. The amount of plankton has decreased further to about 7,000 diatoms per 100 ccm and a very few peridinians, cyanophyceae and flagellates. The principal species is still *Chaetoceros debilis*, but also at surface it has now formed

Table 11 a.

Content of phytoplankton per 100 ccm on Excursion XVI, 3. IV. 1933.

Depth in m	0	5	15
Temperature, ° C	4.2	4.1	5.1
Salinity, ‰	18.38	18.84	32.61
P_2O_5, mg m³	0	0	25
$N — NO_3$, mg/m³	0	0	75
Peridinians	300	..	150
Diatoms	6,900	19,950	7,750
Sceletonema costatum	1,400	5,600	4,550
Chaetoceros debilis	1,660	4,250	4,750
other species	2,600	8,500	5,650
Cyanophycé-colonies	20	50	..
Flagellates	r	2,000	r
Infusorians	..	..	..

Table 11 b.

Experiments on production of matter in surface water from Excursion XVI. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.08
1	
2	
5	
10	0.04
15	0.00

resting spores. Also at greater depths it is now evident that the plankton is about to disappear, only about 7,000 diatoms occurring here. As was the case on the previous excursion the species found here and at surface were the same.

The production of matter could barely be determined and turned out to be about 0.08 mg per l in the surface layers. The weather was sunny or slightly cloudy during the whole experiment.

Excursion XVII, April 12th (Table 12).

The plankton quantity of the surface layers, which originate from the Baltic, has decreased constantly to about 1,500 diatoms. Of small flagellates were found about 5,000 specimens per 100 ccm, but it was impossible to determine whether they were autotrophic or not. The issue of the metabolism experiments was not distinct enough for a precise determination of the production, but the latter was presumably about 0.05 mg glucose per l in the surface layers.

The spring maximum in the Sound off Helsingør has been of extremely short duration. The maximum, initiating about the middle of March, caused an exhaustion of the nutritive salts in the course of one week. After this the production of phytoplankton grows smaller and smaller,

and already less than one month after the occurrence of the maximum it has fallen to quite an insignificant minimum. The proper spring maximum has lasted for about 15 days at most. The production of phytoplankton during this short period does not even stand a comparison

Table 12 a.

Content of phytoplankton per 100 ccm on Excursion XVII. 12. IV. 1933.

Depth in m	0	15
Temperature, °C	5.3	5.0
Salinity, ‰	9.27	14.78
P_2O_5, mg m^3	0	0
$N — NO_3$, mg/m^3	0	5
Peridinians	..	..
Diatoms	1,460	12,150
Chaetoceros debilis	80	2,750
— other species	1,140	6,750
Cyanophycé-colonies	20	..
Flagellates	5,600	r
Infusorians	..	..

Table 12 b.

Experiments on production of matter in surface water from Excursion XVII. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	
1	0.05
2	
5	
10	0.00
15	

with the production of really eutrophic areas as for instance off the coasts of Iceland during the spring maximum when the daily production averages more than 5 times the maximum values found in the Sound off Helsingør.

V. The summer from the middle of April to the end of September.

During the whole of this period the production of phytoplankton was small (see Figure 3, p. 31); at intervals it was so insignificant, that the outcome of the metabolism experiments could not be measured. On the whole the flagellates seem to be the chief organisms of this season. However, the organisms were counted comparatively long time after the samplings, and so it was impossible to decide in this way to which extent chromatophores were found in them. A great part of them, however, must have been autotrophic for it was often possible to establish a distinct if small production of matter although almost no other organisms than flagellates were present in the water. Furthermore, no small number of species of various flagellate groups seem to be completely spoiled by the preservation, so that they cannot be counted at all. A systematic investigation as to the influence of the preservation on the plankton flagellates would be most desirable.

During a long part of this period the Baltic water prevailed at surface, at which time the flagellates were nearly the only producers. This was the case e.g. on the Excursions XVIII—XXIII from April 21th till June 1st. However, on Excursion XXIV, June 12th, a large amount of the diatom *Sceletonoma costatum* were found at surface in a pure Baltic water. But in contrast to most diatoms this is a species that is able to thrive even though only minimum quantities of nutritive salts are present (see further footnote on p. 28).

During the excursions from the end of June to the end of August, No.s XXV—XXXI,

the salinities of the surface water off Helsingør were found to be higher, always above 11 ‰. In this water originating from the Kattegat diatoms also occurred although in small quantities only. The production of matter was decidedly greater during this than during the previous period, but it was still far from being of any great consequence.

In September Baltic water reappeared at surface, and a decrease of the production of matter seemed to follow, however, only one metabolism experiment from this month is fit for use.

Excursions XVIII—XX, April 21st—May 5th (Tables 13—15).

These three excursions may be dealt with collectively. The plankton of the surface layers, which had a typically Baltic character, was extremely poor. Also the amounts of flagellates were small. The metabolism experiments with surface water yielded unsatisfactory outcomes.

Table 13.

Content of phytoplankton per 100 ccm on Excursion XVIII, 21. IV. 1933.

Depth in m	0	15
Temperature, ° C.	5.4	5.0
Salinity, ‰	9.27	14.78
P_2O_5, mg/m³	0	0
$N — NO_3$, mg/m³	0	5
Peridinians	20	..
Diatoms	80	240
Cyanophycé-colonies	..	20
Flagellates	r	r

Table 14.

Content of phytoplankton per 100 ccm on Excursion XIX, 28. IV. 1933.

Depth in m	0	15
Temperature, ° C.	6.4	5.2
Salinity, ‰	8.84	30.52
P_2O_5, mg/m³	0	5
$N — NO_3$, mg/m³	—	—
Peridinians	..	40
Diatoms	420	580
Nitzschia sp.	300	..
Flagellates	1,200	r

In the salt water of 15 m depth various diatoms, *Leptocylindrus danicus* and various *Chaetoceros* species were found on Excursion XX. This plankton has been carried in from the Kattegat by the salt bottom current. On some other excursions of the summer a similar plankton was found in the bottom water. This conveyance of phytoplankton from the Kattegat is undoubtedly of some importance for the nutrition of plankton and bottom animals in the northern part of the Sound. An actual production of phytoplankton in the bottom current off Snekkersten does not usually take place on account of the insufficiency of the light intensity.

Table 15.

Content of phytoplankton per 100 ccm on Excursion XX, 5. V. 1933.

Depth in m	0	15
Temperature, ° C.	8.8	5.7
Salinity, ‰	8.09	31.08
P_2O_5, mg/m³	0	5
$N — NO_3$, mg/m³	—	—
Peridinians	..	60
Diatoms	1,600	3,740
Leptocylindrus danicus	..	960
Chaetoceros decipiens	..	760
Nitzschia sp.	1,520	60
Cyanophycé-colonies	20	..
Flagellates	rr	800

Excursions XXI—XXIII, May 15th—June 1st (Tables 16—18).

Also on these excursions a typically Baltic water was found at surface, but the plankton was somewhat richer, showing up to more than 13,000 flagellates per 100 ccm. Also some small

diatoms occurred, e.g. *Chaetoceros simplex* in a number of 2,400 specimens per 100 ccm on Excursion XXIII. The peridinian *Exuviaella baltica* appeared in quantities of up to 700 individuals per 100 ccm. Judging from the metabolism experiments of Excursion XXII most of the flagellates must have been autotrophic specimens. The metabolism experiments of Excursions XXI and XXIII cannot be used for an ascertainment of the production on account of the uncertainty of the oxygen determinations. The experiments of Excursion XXII showed a daily production in the surface layers of about 0.12 mg glucose. The experiment was carried out in sunny weather.

At 15 m depth a rich plankton of diatoms was found on these excursions.

Table 16.

Content of phytoplankton per 100 ccm on Excursion XXI, 15. V. 1933.

Depth in m	0	5	15
Temperature, ° C.	10.2	10.1	5.3
Salinity, ‰	12.99	13.30	32.16
P_2O_5, mg/m³	0	0	25
$N — NO_3$, mg/m³	0	0	20
Peridinians	500	680	140
Exuviaella baltica	440	680	..
Diatoms	360	280	10,860
Leptocylindrus danicus	..	..	3,040
Chaetoceros species (C. borealis, C. curvisetus, C. constrictus)	..	..	6,260
Nitzschia sp.	280	220	160
Flagellates	12,000	6,800	6,400
Infusorians	60	..	..

Excursion XXIV, June 12th (Table 19).

On this excursion the lowest salinity at surface, 7.68 ‰, was measured. The diatom *Sceletonoma costatum* occurred rather abundantly at surface and 5 m depth, the numbers rising to more than 35,000 individuals per 100 ccm. Unfortunately the bottles for the measuring of the metabolism were lost during the experiment, but a rather considerable production has undoubtedly been going on.

Table 17 a.

Content of phytoplankton per 100 ccm on Excursion XXII, 23. V. 1933.

Depth in m	0	5	15
Temperature, ° C.	10.5	10.7	5.7
Salinity, ‰	8.31	9.54	31.78
P_2O_5, mg/m³	0	0	15
$N — NO_3$, mg/m³	0	0	0
Peridinians	..	100	240
Diatoms	180	800	24,200
Leptocylindrus danicus	..	..	9,000
Chaetoceros species (mostly C. constrictus, C. contortus)	..	..	11,300
Nitzschia sp.	180	800	80
Cyanophycé-colonies	..	20	80
Flagellates	8,000	13,200	1,200
Infusorians	40	60	..

Table 17 b.

Experiments on production of matter in surface water from Excursion XXII. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.12
1	
2	
5	

Excursion XXV, June 19th (Table 20).

The salinity at surface was now 12.23 ‰. Up to about 4,000 diatoms, primarily *Sceletonema costatum*, *Rhizosolenia alata* and *Chaetoceros curvisetus*, were found in the surface layers

Table 18.

Content of phytoplankton per 100 ccm on Excursion XXIII, 1. VI. 1933.

Depth in m	0	5	15
Temperature, ° C	13.8	13.3	5.8
Salinity, ‰	8.15	8.33	33.35
P_2O_5, mg/m³	0	0	15
$N - NO_3$, mg/m³	0	0	0
Peridinians	80	20	350
Diatoms	2,500	920	26,600
Chaetoceros species (mostly C. constrictus, C. contortus, C. curvisetus)	..	..	24,300
Chaetoceros simplex	2,400	800	..
Cyanophycé-colonies	20	..	..
Flagellates	8,000	10,000	rr
Infusorians	..	120	150

Table 19.

Content of phytoplankton per 100 ccm on Excursion XXIV, 12. VI. 1933.

Depth in m	0	5	15
Temperature, ° C	16.8	16.7	6.2
Salinity, ‰	7.68	7.70	33.12
P_2O_5, mg/m³	0	0	5
$N - NO_3$, mg/m³	0	0	0
Peridinians	..	..	..
Diatoms	35,600	32,280	6,600
Sceletonema costatum	35,400	32,200	..
Chaetoceros species (mostly C. curvisetus)	..	..	5,650
Flagellates	17,200	16,400	rr
Infusorians	..	..	..

together with about 20.000 small flagellates. Also at 15 m depth a comparatively rich diatom plankton occurred, pre-eminently various *Chaetoceros* species.

The metabolism experiments with surface water showed a daily production of matter of about 0.16 mg glucose. A distinct production was found even at a depth of 10 m.

Table 20 a.

Content of phytoplankton per 100 ccm on Excursion XXV, 19. VI. 1933.

Depth in m	0	5	15
Temperature, ° C	15.2	14.7	6.3
Salinity, ‰	12.23	13.22	32.84
P_2O_5, mg/m³	0	0	0
$N - NO_3$, mg/m³	0	0	0
Peridinians	..	..	..
Diatoms	3,100	3,720	8,100
Sceletonema costatum	2,180	2,440	950
Rhizosolenia alata	440	240	200
Chaetoceros curvisetus	180	860	5,500
Cyanophycé-colonies	..	20	..
Flagellates	13,200	19,200	6,400
Infusorians	..	..	..

Table 20 b.

Experiments on production of matter in surface water from Excursion XXV. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.16
1	
2	
5	
10	0.08
15	0.00

Excursion XXVI, June 26th (Table 21).

At surface, where typical Kattegat water prevailed as during the previous excursion, were now found about 4,000 diatoms, especially *Rhizosolenia alata* and various *Chaetoceros* species, and further about 16,000 small flagellates.

Table 21 a.

Content of phytoplankton per 100 ccm on Excursion XXVI, 26. VI. 1933.

Depth in m	0	5	15
Temperature, ° C.	11.8	12.0	5.8
Salinity, ‰	..	..	..
P_2O_5, mg/m³	..	..	..
$N — NO_3$, mg/m³	..	..	..
Peridinians	300	160	80
Diatoms	3,760	3,460	22,500
Rhizosolenia alata	720	400	80
Chaetoceros species (mostly C. curvisetus)	1,660	2,540	20,400
Nitzschia delicatissima	460	140	800
Flagellates	16,400	6,800	9,600
Infusorians	..	100	20

Table 21 b.

Experiments on production of matter in surface water from Excursion XXVI. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.10
2	
5	

The metabolism experiments, which were rather unsuccessful, showed a production in the surface layers of about 0.10 mg glucose per l.

Excursion XXVII, July 4th (Table 22).

Also on this excursion Kattegat water was found at surface (salinity 16.19 ‰). More than 8,000 diatoms per 100 ccm were present in the surface layers, almost exclusively *Rhizosolenia*

Table 22 a.

Content of phytoplankton per 100 ccm on Excursion XXVII, 4. VII. 1933.

Depth in m	0	5	15
Temperature, ° C.	18.1	17.7	7.15
Salinity, ‰	16.19	16.65	32.75
P_2O_5, mg/m³	0	0	0
$N — NO_3$, mg/m³	0	0	0
Peridinians	..	40	40
Diatoms	8,240	8,000	19,640
Rhizosolenia alata	7,800	7,680	640
Chaetoceros species (mostly C. curvisetus)	260	200	15,720
Flagellates	5,200	4,000	4,800
Infusorians	..	..	80

Table 22 b.

Experiments on production of matter in surface water from Excursion XXVII. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.26
2	0.22
5	0.21
10	0.13
15	—

alata; besides this there were about 5,000 small flagellates. At 15 m depth were found about 20,000 diatoms, principally Chaetoceros species.

Metabolism experiments with surface water showed a daily production of about 0.24 mg glucose per l in the surface layers. A distinct production was found as far down as 10 m.

Excursion XXVIII, July 12th (Table 23).

Kattegat water was still found at surface, and the plankton corresponded to that found the week before. About 2,000 diatoms occurred at surface, about 5,000 at 5 m depth, in both cases principally *Rhizosolenia alata*. Flagellates were present in numbers of about 25,000 specimens per 100 ccm.

Unfortunately, the metabolism experiments were totally unsuccessful.

Table 23.

Content of phytoplankton per 100 ccm on Excursion XXVIII, 12. VII. 1933.

Depth in m	0	5	15
Temperature, ° C.	19.3	19.5	9.4
Salinity, ‰	..	..	..
P_2O_5, mg/m³	..	..	..
$N — NO_3$, mg/m³	..	..	..
Peridinians	140	120	240
Diatoms	2,020	5,340	7,920
Rhizosolenia alata	1,080	4,860	2,400
Chaetoceros species (mostly C. curvisetus)	180	80	4,520
Cyanophycé-colonies	20	..	..
Flagellates	21,200	20,000	2,800
Infusorians	100	100	..

Excursion XXIX, July 21st (Table 24).

The hydrographical conditions as well as the phytoplankton were unaltered. About 4,000 diatoms, consisting nearly exclusively of *Rhizosolenia alata*, and as much as 8,000 small flagellates were found per 100 ccm in the surface layers. In the bottom current at 15 m depth were counted about 12,000 diatoms per 100 ccm, *Rhizosolenia* also prevailing here.

The average production calculated on the basis of metabolism experiments with surface water from depths of 1, 2 and 5 m was about 0.05 mg glucose; however, the accuracy of these experiments was comparatively slight.

Table 24 a.

Content of phytoplankton per 100 ccm on Excursion XXIX, 21. VII. 1933.

Depth in m	0	5	15
Temperature, ° C.	19.4	18.6	15.0
Salinity, ‰	16.86	16.91	21.53
P_2O_5, mg m³	0	0	0
$N — NO_3$, mg m³	0	10	0
Peridinians	40	80	360
Diatoms	3,920	4,300	11,920
Rhizosolenia alata	3,760	4,200	9,480
Chaetoceros species (mostly C. curvisetus)	..	..	1,240
Flagellates	8,400	3,200	2,400
Infusorians	..	..	..

Table 24 b.

Experiments on production of matter in surface water from Excursion XXIX. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.05
2	
5	

Excursion XXX, August 3rd (Table 25).

Also now Kattegat water was found at surface. Diatoms are near totally absent, but flagellates appear in numbers approaching 15,000 specimens per 100 ccm.

The metabolism experiments showed a daily average production in the surface layers of about 0.13 mg glucose per l.

Table 25 a.

Content of phytoplankton per 100 ccm on Excursion XXX, 3. VIII. 1933.

Depth in m	0	5	15
Temperature, ° C.	18.6	18.3	13.1
Salinity, ‰	12.76	14.22	26.17
P_2O_5, mg/m³	0	0	0
$N — NO_3$, mg/m³	0	0	0
Peridinians	160	60	180
Diatoms	320	100	240
Chaetoceros species	200	80	..
Flagellates	14,800	8,000	3,600
Infusorians	100	60	..

Table 25 b.

Experiments on production of matter in surface water from Excursion XXX. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.12
1	0.10
5	0.16
10	0.04

Table 26 a.

Content of phytoplankton per 100 ccm on Excursion XXXI, 17. VIII. 1933.

Depth in m	0	5	15
Temperature, ° C.	17.9	17.6	17.2
Salinity, ‰	11.13	12.94	20.94
P_2O_5, mg/m³	0	0	0
$N — NO_3$, mg/m³	0	0	0
Peridinians	120	20	140
Diatoms	..	..	280
Sceletonema costatum	..	..	200
Flagellates	10,000	10,400	7,200
Infusorians	160	440	20

Table 26 b.

Experiments on production of matter in surface water from Excursion XXXI. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
0.5	0.16
1	0.14
2	0.19
5	0.13
10	0.04
15	0.00

Table 27.

Content of phytoplankton per 100 ccm on Excursion XXXII, 29. VIII. 1933.

Depth in m	0	5	15
Temperature, ° C.	18.2	18.1	16.4
Salinity, ‰	9.54	9.85	24.10
P_2O_5, mg/m³	0	0	0
$N — NO_3$, mg/m³	0	0	0
Peridinians	..	..	80
Diatoms	..	80	1,680
Chaetoceros species (mostly C. contortus)	..	..	1,400
Flagellates	36,400	32,400	4,800
Infusorians	120	160	..

Excursion XXXI, August 17th (Table 26).

The salinity at surface is 11.13 ‰. The phytoplankton consists nearly exclusively of flagellates, which, however, were very difficult to count owing to the presence of a large quantity of fine detritus. In the surface layers the size order of the amount of flagellates was estimated at about 10,000.

The daily production of the surface layers appeared from the metabolism experiments to be about 0.16 mg glucose per l.

Excursion XXXII, August 29th (Table 27).

The surface water showed a still lower salinity and must be characterized as being nearly

totally of Baltic origin. In the surface layers the plankton consisted almost exclusively of small flagellates in rather large quantities, up to about 36,000 specimens per 100 ccm.

On account of bad weather metabolism experiments could not be carried out.

Excursion XXXIII, September 8th (Table 28).

Also this excursion showed the surface water to be of Baltic origin. Only flagellates occurred in larger quantities, up to about 7,000 specimens per 100 ccm. The metabolism experiments showed a production in the surface layers of about 0.11 mg glucose per l.

Table 28 a.

Content of phytoplankton per 100 ccm on Excursion XXXIII, 8. IX. 1933.

Depth in m	0	5	15
Temperature, ° C.	17.3	17.3	16.7
Salinity, ‰	8.75	8.89	21.56
P_2O_5, mg/m³	0	0	10
$N — NO_3$, mg m³	0	0	0
Peridinians	..	..	220
Diatoms	720	20	220
Sceletonema costatum	660	20	..
Flagellates	7,200	4,400	3,600
Infusorians	400	220	60

Table 28 b.

Experiments on production of matter in surface water from Excursion XXXIII. Duration 24 hours. Production in mg of glucose per l.

Depth in m	mg glucose/l
1	0.12
2	0.10
5	0.05
10	—
15	0.00

Excursion XXXIV, September 22nd (Table 29).

Baltic water was still found at surface. Here the flagellates predominated with about 10,000 individuals per 100 ccm. At 5 m depth the diatom *Sceletonoma costatum* was found in a number of 5,400 specimens per 100 ccm. This species was totally absent at surface.

The results of the metabolism experiments were unfit for use on account of too great variations of the oxygen determinations of the individual bottles.

Table 29.

Content of phytoplankton per 100 ccm on Excursion XXXIV, 22. IX. 1933.

Depth in m	0	5	15
Temperature, ° C.	14.1	14.3	14.8
Salinity, ‰	8.41	8.41	28.29
P_2O_5, mg/m³	0	0	35
$N — NO_3$, mg/m³	0	10	25
Peridinians	120	200	60
Diatoms	20	5,440	320
Sceletonema costatum	..	5,400	..
Flagellates	10,400	13,600	r
Infusorians	700	120	..

Table 30.

Content of phytoplankton per 100 ccm on Excursion XXXV, 2. X. 1933.

Depth in m	0	5	15
Temperature, ° C.	14.4	14.7	15.7
Salinity, ‰	15.76	16.03	24.45
P_2O_5, mg/m³	0	0	10
$N — NO_3$, mg/m³	5	0	10
Peridinians	260	220	20
Diatoms	240	100	460
Sceletonema costatum	..	..	400
Flagellates	r	r	rr
Infusorians	120	..	..

Excursion XXXV, October 2nd (Table 30).

During this last excursion the plankton was poorly represented. The surface water originated from the Kattegat (15.76 ‰). Small flagellates were present but in no great number. An extremely great quantity of detritus hindered a systematic counting of these tiny organisms.

Owing to bad conditions of weather bottles could not be put out for the metabolism experiments. The production must be supposed to have been minimal.

VI. Comprehensive remarks on the annual amount of organic matter produced by the phytoplankton of the Sound off Helsingør.

A. The run of the plankton production.

After a typical winter minimum without any production at all the spring maximum appeared in the middle of March. The comparatively small quantities of the nutritive salts, about 20—45 mg of $N—NO_3$ and 5—10 mg of P_2O_5, respectively, per m^3, which had been accumulated in the surface layers during the winter, were exhausted at once.

It must presumably be taken for granted that the conditions of light have in some way or other been the limiting factor of the production in the Sound throughout the winter months. In Table 31 are given the daily mean figures of cloudiness at 8, 12 and 16 o'clock during the period between February 16th and March 15th at the Lappegrunden Lightvessel at the northern entrance of the Sound. We note that a period of very dark weather from the beginning of February to March 9th was suddenly followed by a bright period, mostly with a thin cover of clouds. This is no doubt a contributory cause of the rich production of phytoplankton found off Helsingør on March 16th, one week after the beginning of the bright period. But another circumstance should also be taken into consideration in this connexion: as mentioned on p. 4 the hydrographical conditions are subject to very great variations. On all excursions from the beginning of January to March 9th the surface water had a very pronounced Baltic character, but on March 16th a typical Kattegat water was found at surface, where there was a salinity of 21.6 ‰. However, it appears from quantitative plankton investigations in the Kattegat that no small quantities of phytoplankton were found throughout the winter of 1932—33; in February and the beginning of March even a rich plankton existed. In Table 32 are stated the plankton quantities in ccm at the Schultz Grund L.V. in the south-western part

Table 31.

Cover of clouds at the Lappegrunden L. V. at the northern entrance of the Sound in the period between February 16th and March 15th, 1933. The numerals are the mean figures of observations at 8, 12 and 16 o'clock. The cover of clouds was estimated by the scale 0—10. From the journals of the Meteorological Institute, Copenhagen.

February		March	
Date	Cover of clouds	Date	Cover of clouds
16	5	1	6
17	10	2	8
18	10	3	10
19	8	4	10
20	3	5	6
21	9	6	7
22	10	7	10
23	10	8	10
24	10	9	10
25	10	10	7
26	10	11	3
27	9	12	4
28	10	13	2
		14	7
		15	5

of the Kattegat from the beginning of January to the middle of March. An open net made of the finest silk gauze (no. 25) was used; the diameter of the net is 30 cm. The hauls were made from 26 m depth to the surface. A similar net was used for the investigations in the Sound where the hauls were made from 15 m depth to the surface. However, the quantities of plankton from these hauls were always quite minimal as compared to those from the Kattegat: from the beginning of January to March 9th the samples made up a fraction of one ccm only and hardly contained any phytoplankton at all. On March 16th, at length, the plankton quantity was 10 ccm, a rather low figure in comparison with the contemporaneous amount in the Kattegat. The surface water from Excursion XIV, on March 16th, originates from the Kattegat, and no doubt the same is the case with the plankton contained in it. However, in the Baltic water the production of phytoplankton began about the middle of March, which appears distinctly from the samples of Excursion XV on March 24th (see Table 10 a on p. 14). The surface salinity was now 11.87 $^0/_{00}$.

Table 32.

Volumes of hauls with plankton net (gauze 25) from 26 m depth to surface, carried out on the Schultz Grund L. V. in the southern part of the Kattegat from January to March 1933.

Date	Volume in ccm
January, 4	5
— , 11	6
— , 19	3
— , 24	5
February, 4	10
— , 11	12
— , 18	20
— , 24	30
March, 9	60
— , 17	200

But what is the reason why practically no production takes place in the Sound until the middle of March although in the Kattegat the production has been going on rapidly for nearly two months? The cause can hardly be a lack of nutritive salts in the surface layers; it is true that only small quantities of these salts were found, but they were absolutely sufficient for a rising production of phytoplankton. Neither can the production be hindered directly by the intensity of light being too low, for at this time of the year there is light enough in the Kattegat to cause a very active production. According to light measurings carried out by Gabrielsen (1934) the light in the middle of bright days must already in January be strong enough to cause a rapid CO_2-assimilation and a consequent propagation of the plankton algae in the surface layers. On the brightest day of January Gabrielsen found a light intensity of more than 7,000 lux in the middle of the day. For 4 hours of the day the light intensity was above 6,000 lux, for 8 hours above 1,500 lux. The optimal assimilation takes place at about 6,000 lux, and an intensity of about half the optimal is found at about 1,500 lux (see Figure 6 on p. 33); so it is easily understood that already during bright periods of January a comparatively large production of phytoplankton can be found to go on in the upmost layers of the Kattegat.

To the plankton algae, which show an all-sided orientation, the light intensity when the rays strike obliquely upon the surface of the water is in fact greater than that measured by means of an ordinary photometer of horizontal orientation. To such an alga of the surface layer the light intensity will be about $^3/_2$ times greater by an angle of incidence of 45° than by an angle of 0° even if the quantity of light penetrating the surface is the same in both cases. By the angle of incidence is in this case understood the angle of incidence in the sea after the rays have been refracted by passing from air to water. An angle of incidence in the sea of 45° corresponds to an angle in the air of 70°. When on a cloudless day the height of the sun above the horizon is 20° or less, which corresponds to the meridian altitude of the sun in the Kattegat during the

first months of the year, the effective light intensity is about $^3/_2$ times greater for the plankton organisms than the intensity measured by a horizontally orientated photometer at the same depth. When the rays fall obliquely, the light will not penetrate so far into the deep but is, so to speak, concentrated in the upmost water layers. In a marine area with stabilized water layers this is of great importance for the production of the plankton algae during the darkest months of the year. However, under conditions like those described here the vertical extension of the productive layer is only small.

In the Kattegat we find a pronounced stratification of the water throughout the year, and therefore not very many of the plankton algae will be carried away from the upper euphotic water layers. Further, the surface water is not very polluted, which can be seen e.g. from the settlement samples. On account of the stability of the water layers and the rather great depths of water comparatively little bottom material is suspended in the Kattegat. An exception to this are of course the areas in the immediate vicinity of the coasts.

In the Sound, however, the sea water from all excursions from the beginning of January to the beginning of March shows a very high degree of pollution by organic and inorganic particles probably originating from the bottom. The quantities present were so large, that a distinct layer settled on the bottom in the water samples. In so narrow a water as the Sound with its prevalence of rapid currents there must obviously be an enormous admixture of bottom material; of course this is particularly distinct during the stormy winter period when the washing of the sea along the shores causes a suspension of bottom material. It should also be remembered that between Copenhagen and Malmo there is a threshold with quite inconsiderable depths of water. Probably the outflow of sewage water from Copenhagen should also be taken into consideration.

At the same time the rapid currents of the Sound will bring about an intenser vertical water movement than in the Kattegat thus probably causing a removal of the plankton algae of the Sound from the euphotic layer at the very surface. These two factors together must be the cause why the production of the Sound in 1933 began as late as the middle of March. Similar or even more pronounced conditions were demonstrated by the author (Steemann Nielsen, 1935, a) to prevail at the coasts of Iceland in spring: here the production generally begins about the middle of May, but on the same latitudes of the Norwegian coast it is found to initiate already about 2 months earlier.

Of course the possibility cannot be disregarded that the conditions of a production of phytoplankton in the Sound may be poorer than in the Kattegat on account of the lower salinities, but this is not very likely.

The hydrographical conditions of the northern part of the Sound being so variable we cannot expect always to find the same conditions of plankton as during the present year of investigation. In the beginning of February 1936 this area showed a comparatively rich phytoplankton, composed principally of the diatoms *Nitzschia delicatissima* and *Sceletonoma costatum*. The comparatively high salinity showed that the water layers originated from the Kattegat. In icy winters quite different conditions will of course influence the production of plankton.

As already mentioned the spring maximum of the phytoplankton of the Sound occurred about 8 days after the beginning of a period with an insignificant cover of clouds, i.e. with a large quantity of light. The conditions of weather must be of decisive importance for the production of plankton during the dark season of the year. As will appear from Gabrielsen (1934, Figure 2, p. 186) we find both in January and June on the darkest days of the months light intensities of about 10 % of those found on the brightest days of these months. But in spite of

this decrease to 10 % on the darkest days of summer we still find a light intensity at surface of about 12,000 lux in the middle of the day and for 10 hours of the day an intensity of more than 6,000 lux, at which the optimal CO_2-assimilation takes place (see Figure 6 on p. 33). However, on the darkest days of January the light intensity at surface is only about 900 lux in the middle of the day; this fact in connexion with the shortness of the day — an intensity of more than 500 lux was found only for 4 hours of the day — means an inferior CO_2-assimilation and, consequently, a small production. In the summer months a very cloudy sky will only cause a lessened vertical extension of the productive layer. This will even be counteracted by the fact that the vertical extension of the very surface layer that exhibits a diminished CO_2-assimilation arising from a too high intensity of the light, will also be lessened (cp. further p. 35). During the experiments on the production of matter at Frederikshavn in the summer of 1931 (Steemann Nielsen, 1932) it even turned out to be impossible to prove the dependence of the vertical extension of the productive layers on the light intensity at surface: the variations in the transparency of the water completely overshadowed the other factor. During the dark months of the year, however, a very cloudy sky will cause a most considerable decrease of the production of plankton even at the very surface.

If the plankton population shows a minimum, as was the case in the Sound during the first months of the year 1933, the occurrence of a long period with good conditions of light is necessary if the phytoplankton shall rise from the minimum to a maximum. Basing his calculations on experiments carried out by Gaarder and Gran (1927) and Gran (1927) the author found (Steemann Nielsen, 1935, a) that a phytoplankton population of about 1—100 specimens per 100 ccm under good conditions in the course of 8 days can rise to a quantity of about 100,000 individuals per 100 ccm, which is a rich plankton. A rate of two divisions in 24 hours is necessary for the rise of such a maximum, and this rate is found only by an active CO_2-assimilation, i.e. only by optimal conditions of light.

However, the presence of a large population of phytoplankton can very well be maintained by comparatively poor conditions of light. Only a slow rate of division is necessary even if allowance is made for a rather considerable loss e.g. through a consumption by the planktonic animals. In this case even a very short period with good conditions of light will cause a considerable production, whereas such a period, as far as the production of matter is concerned, is of inferior importance for a plankton population showing a minimum. During the poor conditions of light in February and the beginning of March 1933 the Kattegat, already containing a numerous population, showed no decrease of the quantity of phytoplankton but a distinct increase (see Table 32 on p. 25) whereas the production of the Sound did not begin at all during this period. Of course it should not be forgotten here that the conditions in the Sound, owing to the poorer transparency of the water and the presumably larger vertical movements of the water, were in themselves less favourable than in the Kattegat.

Immediately after the beginning of the spring maximum the nutritive salts nitrate and phosphate disappear from the surface layers almost at once. On the whole the water layers show an effective stratification all the year round on account of the great differences of salinity from bottom to surface, and so the amount of nutritive salts accumulated at surface in winter is only small. Consequently, the spring maximum in the Sound is of very short duration, about 15 days at most. After this time the nutritive salts are the limiting factor for the production of phytoplankton. From the middle of March till well into October no traces of these salts could be found in the surface layers.

As already mentioned, however, the quantity of nutritive salts is not representative of

the fertility of a marine area, the measurements stating only the momentary surplus of the nutritive salts. The failing to find these salts in the surface layers needs but to mean that the phytoplankton has at once consumed the total amount of regenerated and freshly added nitrate and phosphate. In many freshwater lakes, where a rather intense production is going on throughout the summer, the nutritive salts cannot be found at all at this season.

It must be supposed, however, that the regeneration of the nutritive salts in the surface water off Helsingor together with the adding of fresh quantities is of an inferior size order. The small accumulation of the salts in the surface layers during the winter months is another expression of this supposition. Finally, the insignificant amount of matter produced by the phytoplankton after the spring maximum is a distinct proof that only extremely small quantities of these important salts are available for the plankton algae.

In the water masses near the bottom off Helsingor comparatively large amounts of nutritive salts were still found during the time immediately after the spring maximum of the phytoplankton (Figure 2, p. 7), but from about May 1st the existence of these salts could no longer be established. This does not mean that an actual production of phytoplankton takes place here at a depth of 15 m, for the metabolism experiments showed that the light intensity is here too small for an actual production of algae. But it should be kept in mind that the deeper water layers off Helsingor are constantly shifting owing to their connexion with the waters of the southern Kattegat. The bottom water in the northern part of the Sound must be supposed to originate from water layers near the surface of the Kattegat; it has fallen below the fresher and lighter Baltic water. If the bottom water off Helsingor originated from greater depths of the Kattegat, it would have been found to contain the nutritive salts throughout the summer. The rather considerable amount of diatoms generally occurring in the bottom water in summer also seems to indicate that this water must have come from the surface of the Kattegat. These diatoms have been produced in the surface water of the Kattegat and together with this water they have sunk below the Baltic water. This inflow of phytoplankton from the Kattegat to the bottom water of the northern part of the Sound must be supposed to be going on rather slowly; this supposition is corroborated i.a. by the comparatively low bottom temperatures in summer in the northern part of the Sound.

At Helsingor there was a small production of matter after the spring maximum both when Baltic water and salter water from the south-eastern part of the Kattegat prevailed at surface. However, the greatest production was always distinctly to be found in the latter case. The plankton production of the south-eastern area of the Kattegat is undoubtedly much inferior to that of e.g. the north-western area (cp. Steemann Nielsen, 1932). It also appears from quantitative investigations, which are at present being carried out in Danish waters, that the south-eastern part of the Kattegat is a poor area as compared with the rest of this marine area.

When salter water was found at surface off Helsingor the plankton was composed not only of flagellates but in most cases also of some diatoms, which rarely occurred in very great numbers. When the Baltic water prevailed the plankton consisted nearly exclusively of small flagellates, most of which were presumably autotrophic species. However, on Excursion XXIV, June 12th, was found a large population of the diatom *Sceletonema costatum*. The cause of the isolated abundance of this diatom can only be guessed at[1]).

From the middle of October 1932 traceable quantities of nutritive salts were generally

[1]) There is a slight possibility that this population of *Sceletonema* has originally risen in the sewage water from Copenhagen. The extremely low surface salinity found on Excursion XXIV seems to indicate that this surface water has been passing this city not very long ago.

found at surface; rather large amounts of these salts were observed in the deeper layers already in September 1933 (see Figure 2, p. 7). This fact may undoubtedly be accounted for by an intenser vertical exchange of water, primarily in the Kattegat, arising partly from a cooling of the surface water, partly, and perhaps more particularly, on account of the rougher conditions of weather at this season. By strong westerly winds we may e.g. expect to find a rise of the deeper water in the western part of the Kattegat because the surface water is here pressed in an easterly direction. On the whole the production of matter is of the same size order as in summer (Figure 4, p. 31); a proper autumn maximum does not occur. In the quantity of phytoplankton, however, we find a comparatively considerable rise, at any rate when the surface water originates from the Kattegat, in which case rather large amounts of diatoms are present. Owing to the much smaller daily quantities of light and perhaps also on account of the lower temperature the presence of a much larger number of organisms is necessary for the production of the same amount of organic matter as in the middle of summer. This is a distinct proof that a quantitative determination of plankton cannot be used as a direct measure of the production.

Until the beginning of December the production of matter could be measured by means of metabolism experiments, but it was only in the very upmost water layers that a production was going on so late in the year even under good conditions of light. On Excursion VI, November 22nd, the compensation point for the daily production of matter was found at a depth of 4 m at most although the weather was bright during the whole experiment.

The comparatively large populations of plankton found as late as the end of December show that even in this month the production has not stopped entirely. A sufficiency of bright days gives the plankton population energy enough for subsistence. Undoubtedly the low temperature is also now a condition of the survival of the phytoplankton. From the beginning of the new year practically no phytoplankton was observed in the Sound off Helsingør.

It does not occur every year that comparatively large quantities of phytoplankton may be found in the Sound towards the end of December. According to investigations still unpublished the winter minimum of 1935 was found already in the end of November. As already mentioned the conditions of weather are of decisive importance for the production of phytoplankton during the darker period of the year.

The transparency of the sea water plays a most prominent part as a limiting factor for the production of plankton. Unfortunately, a direct measuring of this factor could not be carried out during the present investigations in the Sound. However, it is easily seen from different circumstances that the transparency of the water off Helsingør is small. The metabolism experiments for instance always showed that the compensation point for the daily production of matter occurs near the surface. Presumably it is never found at greater depths than about 10 m, not even during the brightest period in the middle of summer. A considerable suspension of detritus in the sea water is the cause of this fact. During the counting of the plankton it became possible to estimate the amount of detritus. The latter was nearly always large, sometimes even exceedingly great as for instance in all samples from January and February. Rough weather will suspend a lot of bottom material especially in the shallow water along the coast line. Another active cause of the suspension of bottom material must be the very rapid current that is often met with in the northern part of the Sound.

B. The size of the annual amount of matter produced by the phytoplankton off Helsingor.

In Table 33, and on Figure 3, p. 31, the results of all metabolism experiments have been combined, and here we also find a statement of the average figures of the daily production in the surface layers. On this basis the total monthly production of matter has been calculated per 1 m² of the surface of the sea. However, the accuracy of a great many metabolism experiments being insufficient for a safe determination of the dependence of the assimilation intensity on the depth, the production of matter per m² was calculated as the production in a water column of

Table 33.

The annual production of organic matter pr. m² of the surface of the Sound off Snekkersten 1932—1933.

	Real assimilation of the separate experiments stated in g of glucose pr. m² of the surface of the sea. Dates in brackets	Real assimilation pr. month and pr. m² of the surface of the sea
1932		
October	0.84 (3) 0.40 (11) 0.80 (18) 0.76 (25)	21
November	0.24 (9) 0.77 (22)	15
December	0.08 (6) 0.00 (22)	1
1933		
January		0
February		0
March	0.00 (9) 1.46 (16) 0.44 (24)	19
April	0.32 (3) 0.20 (12) 0.00 (21) 0.00 (28)	4
May	0.00 (5) 0.48 (23)	7
June	0.64 (19) 0.40 (26)	16
July	0.96 (4) 0.20 (21)	17
August	0.52 (3) 0.64 (17)	17
September	0.44 (8)	13
	Total real assimilation of the whole year	130
	÷ Respiration of the phytoplankton (15 %)	20
	Surplus of matter produced by the phytoplankton, stated in g of glucose pr. m² of the surface of the sea	110

4 m, the production of the whole water column being considered equivalent of the average value of the surface layers (0.5, 1 and 2 m). By the use of this method the values arrived at will be approximately of the correct size order.

The compensation point of the Sound off Helsingor will mostly be found at a depth of 5—8 m. In November the compensation point was situated somewhat closer to the surface, and so the depth of the water column has for this month been calculated to be 3 m; for December, finally, it was put at 2 m. From the graphs, Figures 1—6 in Steemann Nielsen, 1932, it is possible to calculate that the production of matter in a water column where the compensation point is found at a depth of 7 m corresponds to the production in a water column of about 4 m, throughout which the assimilation intensity is at its maximum. In the calculation no regard has been paid to the fact that the assimilation intensity is a little below maximum at the very surface.

As the spring maximum is of so short duration, the total production of the month of March is not very great but shows the same size order as in the months of summer and autumn. A particularly poor period in the production of matter seems to occur immediately after the end of the spring maximum: in April and May the monthly production per m² of the surface was only 4—7 g of glucose, but undoubtedly this is primarily due to the prevalence of Baltic water during this period. Otherwise the monthly production per m² of surface ranges between 13 and 21 g of glucose in the period between March and November. In December the production is quite negligible. Of course no great weight should be attached to the individual figures, only the size order being of value.

The total production of matter resulting from the CO_2-assimilation on the part of the plankton algae in the year between October 1st, 1932, and September 30th, 1933, is about 130 g of organic matter, calculated as glucose, per m² of the surface of the sea. If we estimate the simultaneous loss originating from the respiration of the algae themselves at 20 g of glucose[1]), we get an annual surplus in the Sound through the activity of the plankton algae of 110 g of organic matter, expressed as glucose per m² of the surface of the sea.

This is an extremely small production of matter. In the north-western part of the Kattegat at Frederikshavn the monthly production of matter in the height of summer was found to be 150 g per m² (Steemann Nielsen, 1932) or nearly $1^1/_2$ times as great as during a whole year in the Sound off Helsingør. The Sound is a very poor water as far as the production of phytoplankton is concerned. The production is small not only in the water originating from the Baltic, but also in the somewhat salter mixed water that is carried into the northern part of the Sound by southerly currents. The large production of matter found by the author in the north-western part of the Kattegat is no common feature of the whole of this water. The plankton quantities of the Kattegat in summer are also generally found to be largest in the western area. From Table 2 in C. G. Joh. Petersen (1903) it may for instance be calculated that the average plankton quantity of the months of June—October is about 3 times larger in the Læsø Rende in the north-western part of the Kattegat than at the Anholt Knob L. V. Unfortunately Petersen collected no samples in the south-eastern

Fig. 3. The production of matter pr. m² surface of the sea off Helsingør, 1932—1933. The stipulated curve indicates the salinity at the surface.

[1]) Still unpublished investigations by the author in Icelandic waters on the assimilation and respiration of the plankton algae have shown that the respiration is in most cases about $^1/_{20}$ of the optimal intensity of assimilation (temperature about 8° C.). If, therefore, the daily respiration of the plankton algae in the Sound is put at 15 % of the assimilation, we have undoubtedly found the approximate size order.

area of this water off the entrance of the Sound. His investigations in the southern part of the Sound off Rodvig showed that the amounts of plankton found here are always very small. Investigations carried out by Gessner (1933) in the Baltic off the southern entrance of the Sound show that also this area possesses a very poor plankton.

For the Danish waters inside the Skaw we may no doubt put down the general rule: the lower the salinity of the surface water the poorer the production of phytoplankton. This should be understood as follows. A falling salinity of the surface water impedes the admixture to this layer of the salter and heavier water from the lower layers, and consequently there is also a lessened admixture of the important nutritive salts. So it is only natural that we should find the said proportion between the surface salinity and the production of phytoplankton. Furthermore, we may expect to find the largest phytoplankton production of the Kattegat in the western part because in Denmark the west wind is by far the most frequent wind, at any rate outside the spring period. Consequently a rise of the deeper water owing to a pressing away of the surface water must be found principally along the coast of Jutland. Finally, easterly winds will bring about only an insignificant rise of deeper water in the south-eastern part of the Kattegat because this wind at the same time causes a strong outflow of Baltic water through the Sound, thus compensating for the Kattegat surface water that is pressed in a westerly direction by the wind.

VII. The CO_2-assimilation of the plankton algae and its dependence on the intensity of light.

In order to understand the production of matter of the plankton algae it is of decisive importance to know the dependence of the CO_2-assimilation on the intensity of light. As already mentioned metabolism experiments with surface water from the Sound were therefore carried out in the laboratory in the autumn of 1932. This water, which was the same as that used for the metabolism experiments in the Sound, was taken to Copenhagen in thermos bottles, and about two hours after the sampling the experiments began in the Zoo-physiological Laboratory of the University. The duration of the experiments ranges between 14 and 20 hours. This long time was necessitated by the comparatively small production of matter.

The author originally intended to carry out these experiments in the laboratory during the whole period of investigation in order thus to make out eventual differences in the assimilation graphs of the various seasons. This procedure was given up because the production of matter in the Sound turned out to be so small.

For the metabolism experiments in the laboratory I used the following methodics. Small bottles holding 15 ccm and fitted with glass stoppers were placed horizontally on a balancing contrivance in a big aquarium measuring 100 cm in length. Into each bottle was put a small glass ball, which rolled to and fro in time to the movements of the apparatus thus stirring the water. The aquarium was filled with water from the water-tap and the content constantly renewed by running water. One wall of the aquarium was made of glass and in front of this was placed a small aquarium with a glass wall facing the big aquarium. Into the small aquarium was lowered a bulb of 1000 Watt; the water flowing from the big aquarium was led into the small one: in this way the bulb was cooled effectively and the water temperature of the big aquarium could be kept at a constant level. The balancing contrivance, on which the bottles were placed in pairs at different distances from the front glass, was kept working by slowly running water, which alternately filled and emptied a small water tank. Behind the front pair

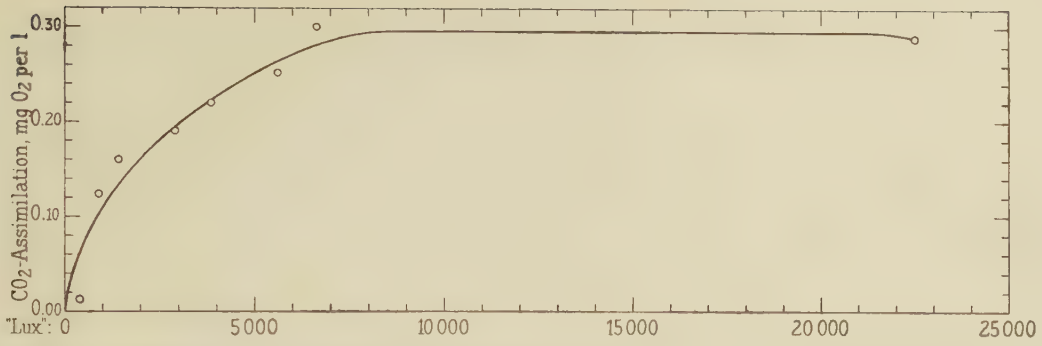

Fig. 4. The CO_2-assimilation (real) during the laboratory experiments October 3rd—4th, 1932 (cp. table 34).

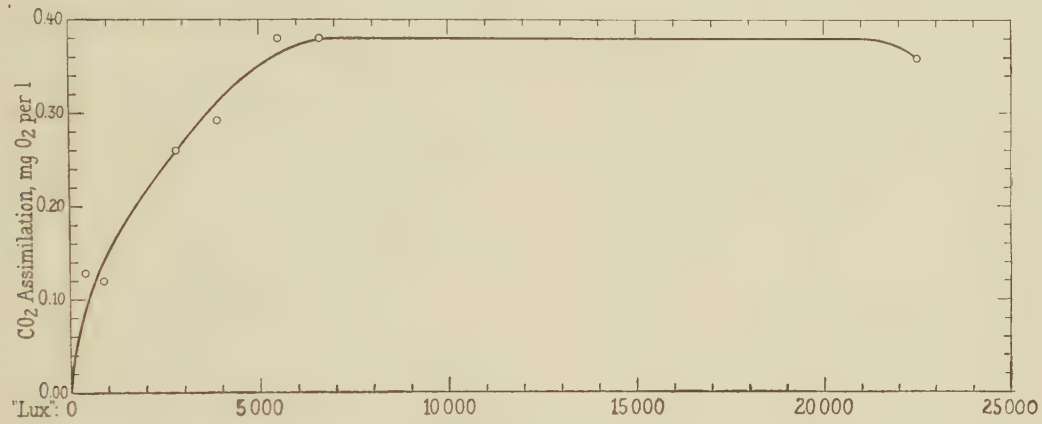

Fig. 5. The CO_2-assimilation (real) during the laboratory experiments October 18th—19th, 1932 (cp. table 35).

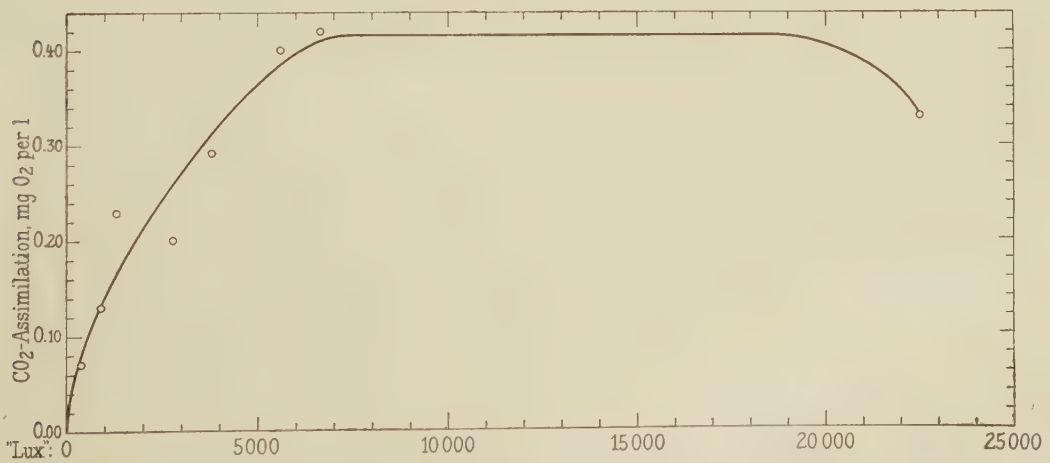

Fig. 6. The CO_2-assimilation (real) during the laboratory experiments October 25th—26th, 1932 (cp. table 36).

of bottles was placed a silk screen in order to lower the intensity of light. In this way experiments could be carried out simultaneously by intensities ranging between 490 and 22,500 lux. The intensity of light was measured by means of a photometer of Boysen-Jensen's construction (1932). This photometer principally registers the red part of the spectrum.

In Tables 34—36 and Figures 4—6 are stated the results of three experimental series from October 1932. The experiments were made on October 3rd—4th, 18th—19th and 25th- 26th. The temperature during the experiments was 12—13° C. or approximately the same temperature as was found in the surface water off Helsingor at this season (12.7—10.0° C.).

Table 34.

Laboratory experiments October 3rd—4th, 1932, with surface water from Snekkersten (content 6,420 diatoms per 100 ccm). The values for the CO_2-assimilation (real) and the respiration are given in mg O_2 per l. Duration of the experiments 14 hours.

Initial O_2 content 1. 9.62, 2. 9.64 } 9.63

"Lux"	O_2 content	Real assimilation
22,500	1. 9.86	0.29
	2. 9.82	
6,600	1. 9.86	0.30
	2. 9.83	
5,500	1. 9.80	0.25
	2. 9.80	
3,800	1. 9.77	0.22
	2. —	
2,800	1. 9.74	0.19
1,380	1. 9.71	0.16
900	1. 9.66	0.12
	2. 9.67	
490	1. 9.52	0.01
	2. 9.59	
dark	1. 9.55	Respiration
	2. 9.54	0.08

Table 35.

Laboratory experiments October 18th—19th, 1932 with surface water from Snekkersten (content 5,880 diatoms per 100 ccm). The values for the CO_2-assimilation (real) and the respiration are given in mg O_2 per l. Duration of the experiments 17 hours.

Initial O_2 content 1. 9.15, 2. 9.13 } 9.14

"Lux"	O_2 content	Real assimilation
22,500	1. 9.50	0.36
	2. 9.46	
6,600	1. 9.50	0.38
	2. 9.49	
5,500	1. 9.50	0.38
	1. 9.42	0.29
3,800	2. 9.39	
	1. 9.38	0.26
2,800	1. 9.24	0.12
900	2. (9.05)	
	1. 9.24	0.13
490	2. 9.25	
	1. 9.11	Respiration
dark	2. 9.12	0.02

The assimilation graphs drawn on the basis of the three experimental series show a high degree of congruity. Of course the run of the graphs by the lowest intensities could not be determined with absolute certainty because the sources of error would here come to play too prominent a part. However, this fact is of no significance whatever for the purpose of the present investigations. For the same cause it was impossible to determine the precise situation of the compensation point, but this is also of less importance because the experiments were carried out with raw plankton. It could not, for all that, be made out how great a part of the respiration is due to the plankton algae and how great a part to the heterotrophic organisms, particularly the bacteria, which generally seemed to occur abundantly.

At a light intensity of 6,000 to 7,000 lux the CO_2-assimilation graph reaches its optimum. At about 1,500 lux the intensity of the CO_2-assimilation is half the optimal. By the highest light

intensity used in the experiments, 22,500 lux, an optimal assimilation was observed during the first two series of experiments, the third series showing a pronounced falling off of the intensity of assimilation. This was also most distinctly to be seen from another series of experiments on November 22nd—23rd, which has not been considered here because the development of some small air-bubbles reduced the accuracy of the results.

Later investigations at Iceland, the results of which will be published elsewhere, have shown that the optimum of the CO_2-assimilation is found between approximately 6,000 and 20,000 lux. By higher intensities the assimilation decreases. So the highest intensity used in the present investigations in the laboratory comes very near to the upper limit of the optimal assimilation, and it is no wonder that some series of experiments exhibit an optimal assimilation while others show a distinct decrease of the intensity. The intensity at which the light begins to check the CO_2-assimilation of the plankton algae will presumably be subject to variations according to the composition of the plankton and the temperature.

We do not know for certain whether or not the decreasing effect on the assimilation of a great intensity of light is confined to rays of a certain colour. It appears from CLARKE's experiments (1936) that the blue (and perhaps green) rays are noxious by great intensities. At depths of 40 and 60 m in the Sargasso Sea where only blue and green rays are found in great quantity he found the intensity of assimilation to be distinctly lower than at 80 m depth. No investigations have been carried out to the effect of showing whether rays of great intensity in the red part of the spectrum will affect the plankton algae in a disadvantageous way; however, this is not very likely. It is a well-known fact that it is nearly exclusively the rays in the blue part of the spectrum that will tend to decompose the chromatophores of the plants.

Table 36.

Laboratory experiments October 25th—26th, 1932 with surface water from Snekkersten (content 9,200 diatoms per 100 ccm). The values for the CO_2-assimilation (real) and the respiration are given in mg O_2 per l. Duration of the experiments 17 hours.

Initial O_2 content $\left.\begin{matrix} 1. & 8.91 \\ 2. & 8.92 \end{matrix}\right\}$ 8.92

"Lux"	O_2 content	Real assimilation
22,500	1. 9.38	0.33
	2. 9.33	
6,600	1. 9.46	0.42
	2. 9.44	
5,500	1. 9.42	0.40
	2. 9.43	
3,800	1. 9.31	0.29
	2. 9.34	
2,800	1. 9.23	0.20
1,380	1. 9.27	0.23
	2. 9.24	
900	1. 9.16	0.13
	2. 9.16	
490	1. —	0.07
	2. 9.10	
dark	1. 9.05	Respiration
	2. 9.01	?[1]

[1]) Apparently there is a distinct increase of oxygen in the bottles that have been kept in the dark. This will undoubtedly be due to an error made during the experiment. Possibly I have forgotten to shake the bottles with the oxygen samples from before the experiment one hour before the adding of H Cl, a manipulation which was otherwise carried out in all cases. If this is the case it explains the low oxygen values of the original water samples.

In the Danish in-waters the light, even in the middle of summer, will be too intense for the plankton algae only in the very upmost water layers, down to a depth of 1 m at most. This is primarily due to the large quantities of matter always suspended in the water.

VIII. Summary.

By means of metabolism experiments with surface water with a natural content of plankton the production of organic matter during one year, 1932—1933, was determined in the northern part of the Sound.

The annual production of matter (see Figure 3, p. 31) was extremely low (110 g of organic matter calculated as glucose per 1 m^2 of the surface of the sea). This is only about $^2/_3$ of the production of one summer month in the north-western part of the Kattegat. The point of compensation for the daily CO_2-assimilation and respiration was generally found rather near the surface and never at greater depths than about 10 m. This is due to the poor transparency of the water.

After a winter minimum, beginning with the new year, without any production of phytoplankton the spring maximum occurred about the middle of March. In the Kattegat, however, comparatively large quantities of phytoplankton were observed throughout the winter, and in February a rapid growth of the phytoplankton could be established. The cause of the late beginning of the production in the Sound must be the very poor transparency of the water of this locality during the winter months in connexion, no doubt, with a more extensive movement of the water bodies than in the Kattegat. Although the water layers of both areas are effectively stabilized throughout the winter, the vertical movement must be supposed to be at any rate of some importance in the Sound owing to the very rapid current generally prevailing here. However, an actual intermixing with the deeper water bodies does not take place; that is why we find a small production throughout the summer. Neither are fresh quantities of the nutritive salts carried to the surface in other ways. The phytoplankton is particularly poor when typical Baltic water is found at the surface of the Sound.

In the autumn of 1932 traceable quantities of the nutritive salts were found in the surface water from October. But also during this period the production of phytoplankton was of a rather low standard.

Determinations of the intensity of assimilation by artificial light in the laboratory showed an optimum by intensities between 6,000 and 20,000 lux. By an intensity of about 1,500 lux the intensity of the assimilation is about half the optimal. By light intensities above 20,000 lux the assimilation decreases. It is the blue rays in great intensity that are noxious to the chromatophores.

On bright days there will already in January be light enough in the surface layer to cause an active CO_2-assimilation. If the other conditions are good, such as the stability and the transparency of the sea water, a rapid production of phytoplankton takes place. This is the case in the Kattegat, but not in the Sound.

In summer a very overcast sky causes but a slight decrease of the production of matter on the part of the phytoplankton in the Danish waters: here the differences in the transparency of the sea water are of greater importance. During the dark months of the year, however, a very overcast sky will nearly bring the production of phytoplankton to a complete stop.

IX. Litterature.

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